"torula" stage of one of these higher fungi. Full descriptions and figures are given by the author.

The form *Mycoderma cerevisiæ* was thoroughly examined. The author's results confirm what is known as to its aërobian characters. Statements as to its identity with *Oïdium lactis* were not only not confirmed, but the author grew these two forms side by side, and maintains their distinctness. Nor could he obtain spores in this fungus, thus failing to confirm earlier statements to the contrary. He regards it as probable that oil-drops have been mistaken for spores; he also finds that in later stages of fermentation by this organism a strong oily-smelling body is produced.

With regard to *Bacterium aceti*, the author has nothing new to add. A point of some interest was the repeated production of acetic ether, which scented the laboratory when this Schizomycete was growing in company with the small white aërobian top-yeast referred to under (β). As this phenomenon was found to have nothing to do with the question being investigated, the author did not pursue it further. It seemed probable, however, that the yeast produced alcohol, which the Schizomycete, in presence of oxygen, partially oxidised, and that the fragrant ether was produced by interaction of the products.

With regard to the other forms found, the author was chiefly concerned with testing their relations to the important and essential organisms. It need only be remarked here that hanging-drop cultures of *Dematium pullulans* were very successful, and that some of the moulds, and at least one *bacillus* (of which the spore-formation, &c., were traced also), were traced to the ginger used in the manufacture of the well-known beverage.

The author hopes very shortly to have the honour to lay before the Society a full account of his research, of which the above is only a brief notice. The fuller account will contain detailed descriptions, as well as figures of the apparatus, mode of culture, &c.

II. "Studies in the Morphology of Spore-producing Members. Preliminary Statement on the Lycopodinæ and Ophioglossaceæ." By F. O. Bower, F.R.S. Received November 27, 1891.

It is currently held that the sporophyte, or neutral generation in archegoniate plants, is the result of elaboration of the zygote: that while in certain Algæ the zygote simply divides to form a number of spores (carpospores), in the lower Bryophyta there has been a differentiation of an external, sterile, and protective wall, distinct from the

internal mass of spores. The higher Bryophyta show a larger proportion of sterile tissue, which in them composes the seta, columella, and wall, while the sporogenous tissue is comparatively reduced in bulk, though still forming one united band. In the vascular plants the proportion of sterile tissue to the sporogenous tissue is larger still; elaboration of form has in them resulted in the production of appendicular organs, while the sporogenous tissue is partitioned off into small, isolated masses, or even single cells, these being situated in members which are commonly called *sporangia*. The series from the lowest to the highest of these types probably illustrates the essential points in the actual process of evolution of the higher from the lower forms; from it we recognise that the ascending series shows a *progressive sterilisation* of the tissues of the neutral generation, and also an increasing *elaboration of external form and internal structure*, the two lines of progress going, in a measure, hand in hand.

It is obvious that, if the progression were as above stated, the function of the spore-production preceded the vegetative functions of the sporophyte in point of time; spore-producing members may, in this sense, be termed *primary* from the point of view of descent, and the vegetative members, *secondary;* the morphology of spore-producing members should accordingly take precedence of the morphology of vegetative members, and an exhaustive study of the former is therefore specially necessary.

The widest gap in the series of those plants which show antithetic alternation is believed to be that between the Bryophyta and the Vascular Cryptogams; to bridge over this gap between plants with simple form and united archesporium, and those with complex form and separate small archesporia, is the most clearly outstanding problem of morphology. Of intermediate forms there are practically none known; but it is believed by the author that a careful examination of the spore-producing members of the lower vascular plants, with special regard to their development, will best lead to some clear opinion as to the way in which the transition may have taken place. A comparison of such plants as form natural series may demonstrate progressions of elaboration and sterilisation, which may be regarded as *analogous* to the progression from the Bryophyta to the Vascular Cryptogams. Such an analogous progression is believed to be found in the Lycopodinæ and Ophioglossaceæ. Even if this analogy be not admitted, the further investigation of the sporangia of certain rarer and less known Vascular Cryptogams, to be described below, will be of sufficient interest to justify the work.

The present preliminary statement will refer to the Lycopodinæ and Ophioglossaceæ only.

The simplest known type of the former is *Phylloglossum*, which I agree with Dr. Treub in regarding as a truly rudimentary form.

The sporophyte consists of two parts:—(i) the *protocorm*, with its protophylls and roots, and (ii) the *strobilus*, with sporophylls and sporangia. The transition from (i) to (ii) is usually sudden, and without intermediate steps.

The sporangium of *Phylloglossum*, as regards its external form, is intermediate in character between that of *Lycopodium Selago* and *L. alpinum*; the archesporium consists of a single row of about six cells, only one of which appears in each radial section; in this, *Phylloglossum* is like *L. selago*. The whole strobilus also, when mature, is closely similar to that of a simple *Lycopodium*, and the development of the sporangium corresponds also in all essential points.

Several species of *Lycopodium* have been examined as regards the structure and development of the sporangium; previous investigators have figured only radial sections; it is obvious that radial, transverse, and tangential sections in various stages will be necessary for the complete description of the development of so large and complex a body; the result of comparison of such sections has been—(i) to acquire a clear knowledge of the form and composition of the archesporium, and (ii) to show that this varies in different species of the genus.

Two cases will be briefly described, viz., *L. Selago* and *L. clavatum*.

In the former the sporangium appears as a rather narrow, sharply convex outgrowth from the upper surface of the sporophyll; the archesporium consists of a single row of cells, of which one only appears in the radial section; the smallest number seen in the tangential sections is seven, which may possibly be referable in origin to three parent cells. While the archesporium increases largely with age, neither the stalk of the sporangium nor the sub-archesporial tissue increases greatly in bulk, so that the mature sporangium assumes the form of a slightly curved sausage, attached by a comparatively slender and long stalk.

In *L. clavatum* (to which also *L. alpinum* closely corresponds), the sporangium appears as a broad, only slightly convex out-growth; the archesporium does not consist of a single row of cells, but usually of *three rows*: thus three cells would appear in each radial section: both radial and transverse sections show that these are not readily referable in origin to a single parent cell. In tangential section it appears that ten or more cells may be present in each row. As the archesporium grows, the stalk remains short and bulky, while the sub-archesporial mass develops as a large pad of sterile tissue, which arches the sporogenous tissue convexly upwards. The whole sporangium when mature is thus strongly curved, and is inserted on the sporophyll by a short and massive stalk. These characters are important for comparison with *Ophioglossum*.

It may be added that, so far as observations have yet been made on

Selaginella, its sporangium appears to be comparable to the *Selago* type of *Lycopodium*, though with differences of detail, which need not now be specified.

The results obtained by observation of the Lycopodinæ have been used for purposes of comparison with the Ophioglossaceæ, and the result is a view as to the real nature of the so-called "fertile frond." This structure has long been a morphological crux, and various opinions have been held with regard to it, which severally make demands upon morphological faith. The theory now to be put forward is, *that the "fertile frond" is an elaborated and partitioned sporangium*, homologous with the smaller and non-partitioned sporangium of the Lycopodinæ. Developmental evidence will now be adduced in support of this theory.

The "fertile frond" of *Ophioglossum vulgatum* arises as an outgrowth of the upper surface of the "sterile leaf": not, it is true, at the base, but rather below the middle: the cell-divisions do not correspond in detail to those in the young sporangium of *Lycopodium*, but I do not think that, at the present day, this will be reckoned as a material ground for rejecting an homology. There is in fact, at first, a single initial cell, with rather irregular segmentation, but the apical growth of the elongated and upward directed "fertile frond" passes over shortly to the type with, apparently, four initials.

The origin of the archesporium and sporogenous tissue has been traced in *Ophioderma pendulum* by the help of material supplied through the kindness of Dr. M. Treub. In this plant, as in *Ophioglossum*, the sporangia are deeply sunk in the "fertile frond," and form a longitudinal series running along each lateral margin of it, and extending to the extreme apex. Transverse sections in the young state would thus show the archesporia at the most curved points of the elliptical section. In the youngest transverse sections which were observed, the archesporial tissue appears composed of many cells, and it is doubtful whether all be referable to a single parent cell; but, seeing that this section would correspond to what is seen in a radial or a transverse section of the sporangium of *Lycopodium*, and that there is a difference (*e.g.*, between *L. selago* and *L. clavatum*) as to the reference of the archesporium to a single cell in such sections in different species of that genus, this question cannot be considered as a vital one.

The archesporial tissue thus seen in transverse sections of the young "fertile frond," is found in tangential and radial sections to be *a continuous band*, which extends along each margin to the apex; it is believed to correspond to the curved band of archesporial tissue in *Lycopodium*, and may, therefore, be styled the *potential archesporium*. But whereas in *Lycopodium* the whole of this tissue forms spores, only parts of it develop as sporogenous tissue in *Ophioderma:* for, as

it grows older, the archesporial band becomes differentiated into (*a*) *sporogenous masses*, which soon are densely filled with protoplasm, and develop further into spores, as already known, and (*b*) *sterile tissues*, which intervene between these, and develop into the septa between the sporangia, together with part of the tapetum.

A similar continuous band of hypodermal tissue has been found in *Ophioglossum* also, and is believed to be the continuous *potential archesporium*.

If the tissue thus recognised in *Ophioderma*, and, with less certainty, in *Ophioglossum*, be the potential archesporium, and correspond to the curved band of archesporium in *Lycopodium*, then the whole "fertile frond" of *Ophioglossum* and *Ophioderma* must be homologous with the sporangium of *Lycopodium*: the central tissue of the "fertile frond" will be the counterpart of the sub-archesporial mass of *Lycopodium*, and the whole will illustrate *the result of elaboration, partial sterilisation, and consequent partitioning of the sporangium*.

But it will further be pointed out that the Ophioglossaceæ, which are a natural family with obviously close affinities, illustrate the progress of elaboration of the sporangium by still further steps within their own circle of affinity. This will appear on comparison of *Helminthostachys*, of which I have received well-preserved specimens, collected in Ceylon by Mr. J. Bretland Farmer. Here the "fertile frond" is not so simple as in *Ophioglossum*; its homology is, however, demonstrated by its position, and by the fact that its main features of early development are similar. The spore-producing parts are borne along the two lateral margins; but, instead of the large sporangia deeply sunk in the tissue, as in *Ophioglossum*, their place is taken in *Helminthostachys* by branched outgrowths, each of which may bear a number of smaller sporangia; these branched outgrowths may be styled provisionally the *sporangiophores*. They are not disposed with strict regularity, but are restricted to the margins of the "fertile frond," and thus topographically they replace the sporangia of *Ophioglossum*: functionally they do the same, for part at least of their tissue becomes sporogenous. The development of them has been traced, but it need not now be described in detail; it will suffice to make the general statement that it shows nothing incompatible with the theory above put forward. The sporangia correspond in their development and main features to those of *Botrychium*. A comparison of *Helminthostachys* with *Ophioglossum* would point to the conclusion that in the former is seen a further phase of *elaboration*, *partial sterilisation*, and *partitioning*. If the archesporium of *Ophioglossum* were further subdivided by sterilised partitions, and the several parts raised by vegetative outgrowth of tissue, so as to project beyond the general surface, the result would be something like that which is actually seen in *Helminthostachys*.

A somewhat similar view, though different in some details, may be held also in the case of *Botrychium*.

There are, however, other facts relating to both the Ophioglossaceæ and Lycopodinæ which are obvious externally, and which are, I think, most readily explained on an hypothesis of elaboration and partial sterilisation: these will now be briefly alluded to. In certain species of *Lycopodium* (*e.g.*, *L. Selago*) there is no marked difference between the foliage leaves and the sporophylls: in many other species the difference is only slight. It may be noted that in certain species (*e.g.*, *L. alpinum*) towards the base of the strobilus the young sporangia show gradual reduction in size, these leading on to cases of complete abortion. At the apex of the strobilus also there is often a similar reduction of the sporangia (*Phylloglossum*, *L. clavatum*, &c.), the uppermost leaves being thus sterile. Again in *L. Selago* and some tropical species, sporangia are borne on certain zones of the plant, while on alternating zones there are only sterile leaves. In the Ophioglossaceæ also the leaves of weak plants are frequently sterile, and bear no matured "fertile fronds": examination of these, however, frequently discloses a small and abortive "fertile frond" occupying the position of the normal one. How are these organs in the Lycopods and *Ophioglossum* to be explained unless they be regarded as the reduced and abortive remains of parts which under other circumstances might have come to functional maturity? They are, in fact, evidence of further *sterilisation*, though in this case it is not partial, but extends even to the whole sporogenous tissue of certain sporangia.

Putting together these last facts, and the developmental data previously stated, the following seems to me to be a reasonable theory, which will, I think, throw some light upon the probable relations of the Lycopodinæ and Ophioglossaceæ from the point of view of descent:—

The primeval strobilus consisted of axis, sporophylls, and sporangia: any of these parts was capable of further elaboration, and the balance of them *inter se* might thus have been modified.

In *Phylloglossum* there is a small strobilus which springs directly from the protocorm. This whole strobilus is probably of a primitive type, and may correspond to an elaborated sporogonial head (see below).

In the various species of *Lycopodium* the whole plant (exclusive of the protocorm, &c.) represents an extended and branched form of such a strobilus, of which many of the sporophylls have been sterilised, and appear as the foliage leaves, having no sporangia. The whole plant shows a prevalence of development of the axis over the leaves or sporangia.

In the Ophioglossaceæ the converse is the case; the axis remains relatively small (except in *Helminthostachys*, where it is seen as the

horizontal rhizome), while the sporophylls (= "sterile fronds") and sporangia (= "fertile fronds") are largely extended, the elaboration of the two showing a remarkable parallelism. In *Ophioglossum vulgatum*, where the sporophyll is simple though much larger than in *Lycopodium*, the sporangium ("fertile frond") is elongated and partitioned by the sterilisation of transverse bands of the potential archesporium. In *Ophioderma* (as also in some species of *Ophioglossum*) the sporophyll is irregularly lobed, while the sporangium ("fertile frond") is occasionally branched. In *Helminthostachys* the sporophyll is branched, and the whole sporangium ("fertile frond") is also branched occasionally; but in addition it shows that elaboration above described, and it may be looked upon as the result of further partitioning of the archesporium, and outgrowth of separate parts of the superficial tissues as the "sporangiophores." Finally, in some species of *Botrychium* the sporophyll and sporangium ("fertile frond") are both repeatedly branched, and show the furthest divergence of the whole series from their simpler prototypes, which are the sporophyll and sporangium of the Lycopods.

In this view thus stated there is nothing incompatible with what might be expected on *a priori* grounds; on the contrary, there is good reason to look upon such a progression as one of the natural ways in which the number of spores produced might be increased, such increase in number being obviously beneficial. Taking the simple strobilus as the starting point, one method would be the elongation of the strobilus, and increase in the number of sporangia produced upon it, they remaining individually of relatively small size; this is the type seen in the Lycopods. A converse method would be to increase the individual size of the sporangium, while the number of sporangia might remain small and be matured at intervals; this is exemplified by the Ophioglossaceæ. But if simple enlargement of the sporangium took place, without subdivision of the archesporium, the rapid supply of nourishment to the enlarged mass of growing spores would be difficult, while at the period when the sporogenous mass is semi-fluid, owing to the cells separating from one another, and floating freely in fluid, the sporangium would run great risk of mechanical injury from without, and a single puncture of the wall of the large sporangium would ruin the whole. These difficulties are all avoided by partitioning of the sporangia; the sterile tissue of the partitions, while strengthening the whole, would, together with the increased sub-archesporial mass, serve the more readily to bring nourishment to the developing sporogenous tissue; the transfer is further provided for by the vascular system which extends upwards through the centre of the "fertile frond," and even into the sporangiophores of *Helminthostachys*.

The effect of this theory would be to bring the Ophioglossaceæ

systematically nearer to the Lycopodinæ; this relationship has been recognised by various writers on other grounds, and the characters of the sexual generation will even help to support this nearer affinity.

A special interest will now centre round a small and very rare plant, viz., *Ophioglossum Bergianum*, one dried specimen of which I received from Professor MacOwan. It appears to show points of affinity both to *Phylloglossum* and *Ophioglossum*. While it is obviously an *Ophioglossum*, it shows (1) in the form of the leaf and the general habit, (2) in the fact that more than a single leaf is exposed at once, (3) in the low point of insertion of the "fertile frond," and (4) in the small number of partitions in it (sporangia, 8—12), characters which suggest that its further investigation would probably disclose facts of the greatest importance.

The relation of *Isoetes* to our series will naturally be a close one; just as the plant of *Ophioglossum* may be looked upon as a vertical strobilus, of which the large sporophylls are developed in slow succession, so also may *Isoetes* be regarded as a simple vertical strobilus, but the leaves are more numerous; the leaf (sporophyll) is relatively large, though simple. The sporangium is, in form, like a flattened cake, inserted on the upper surface of the leaf, near its base; it also is partitioned, more or less completely, and Goebel has shown clearly in his drawings how the hypodermal tissue, which may here also be styled the potential archesporium, becomes differentiated into sterile trabeculæ and sporogenous cells. To this differentiation I should assign a similar interpretation to that in the Ophioglossaceæ; the sporangium is, however, less elaborated, and its size and prominence are not such as to have led to its sporangial character being lost sight of.

Quite recently, on examining the fine series of sections of *Lepidostrobus* in the British Museum, I have found processes of sterile tissue which spring from the base of the sporangium, and project far into the mass of spores; these appear to be comparable to the trabeculæ of *Isoetes*, though differing in points of detail.

I do not think it desirable as yet to express opinions as to the bearing of this work upon the other Ferns. At present I am disposed to think that the Ophioglossaceæ and *Isoetes* are in an intermediate position between the Lycopods and other Ferns, and that their affinity to the former is certainly quite as close as to the latter.

The Psilotaceæ are probably a separate series, remote from both; they will be dealt with on a later occasion.

We have seen how the Ophioglossaceæ illustrate, according to our theory, the elaboration and partitioning of a sporangium, which in the Lycopods is relatively small and simple, and has an undivided archesporium. It is suggested that in this series there may be seen a progression *analogous* to that by which the vascular plants originated from some Bryophytic forms with simple sporogonial head. Take,

for example, the strobilus of *Lycopodium*, or of *Equisetum;* it is not difficult to see how, from a Bryophyte with an archesporium such as that of *Anthoceros*, the strobilus might originate from the sporogonial head, by partitioning off the archesporium (such as that seen in *Ophioderma*), and outgrowth of new members from the surface (such as are seen in *Helminthostachys*). The details of the process might doubtless be different; it is not even contended at present that this may have been the mode of origin of *all* the stocks of Vascular Cryptogams. But the point is that *an elaboration similar to that which may be traced in the spore-bearing members of the Lycopodinæ and Ophioglossaceæ of the present day might, if carried out in a sporogonium such as that of* Anthoceros, *result in a strobilus not unlike those of* Equisetum *or* Lycopodium. The gap between the Bryophytes and Vascular Cryptogams would thus be bridged over by a hypothesis based upon analogy. I am fully aware how open such a hypothesis is to criticism, but I think that it is better, after careful and widely extended comparative observation, to put out the hypothesis than to be content with no clear hypothesis at all. More especially is this so in the present case, where no intermediate types are at present known to exist, and where we have no special reason to expect that such types will be discovered.

The above description makes it evident that a revision of terminology of spore-bearing members will be necessary; if the spore-bearing member of the Ophioglossaceæ be homologous with the sporangium of *Lycopodium*, it is obviously undesirable to call it a "fertile frond." It could not, however, be termed a sporangium without violence to the meaning of this word. I have not yet arrived at a conclusion on such points as these, and shall defer the definition of the terms to be used until the memoir, of the contents of which this is a short and partial preliminary statement, shall be ready for presentation to the Society.

In conclusion, no reference has been made in this statement to the higher plants. Clearly the enunciation of new views with regard to the lower vascular plants must affect opinions as to the morphology of the higher. The interpretation of these will ultimately have to depend upon conclusions drawn from the study of the lower types. Hitherto it has been the practice to read the morphology of the lower forms in terms of the morphology of the higher; the converse will have to be ultimately adopted. Nevertheless, I have abstained at present from touching upon such questions as these, partly because such discussions would obscure the present issues, partly because the time has hardly yet come for any general statement.

The Society adjourned over the Christmas Recess to Thursday, January 14, 1892.